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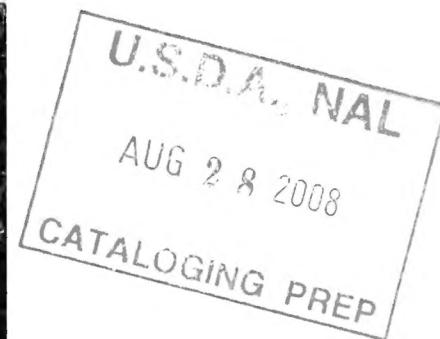




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# OBSERVATIONS ON PINE SUSCEPTIBILITY TO WEEVILS

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PACIFIC SOUTHWEST  
FOREST AND RANGE  
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# OBSERVATIONS ON PINE SUSCEPTIBILITY TO WEEVILS<sup>1/</sup>

By R. Z. Callaham, Geneticist

Research on the resistance of pines to their insect enemies has been under way at the Institute of Forest Genetics for nearly twenty years. The first work was on susceptibility to resin midge (Austin *et al.*, 1945). After World War II, John M. Miller reactivated this line of research. His initial work concerned the resistance of species and hybrids to the pine reproduction weevil (Cylindrocopturus eatoni Buch.) (Miller, 1947; 1950). This killer of young pines has devastated plantations in California.

This weevil can be observed in its natural attacks in the nursery and plantations of the Institute. Thus, every year mortality in progenies set out for genetic tests but subjected to weevil attack can be studied. Miller made observations on natural mortality in the nursery beds at the Institute in 1949 and 1950. He observed variation in susceptibility of inter- and intraspecific hybrid progenies to weevils. His record supplemented with my additional observations during 1952 and 1953 are the basis for this paper.

The data obtained are fragmentary; yet, the results when added together are quite significant. They confirm the relative susceptibility of species. They provide a basis for inferring differences in susceptibility within species. They show a different pattern of attack by the weevils on trees which survive versus those which succumb. Most important, they show that well-conceived studies, primarily designed to study resistance to weevils, are requisite for determining insect resistance and that the inadequacy of merely observing the results of uncontrolled attacks is soon apparent. Yet the approach has merits (1) as a means of confirming more controlled but more unnatural tests and (2) as a means of indicating new avenues for controlled investigation.

Miller and I observed this natural weevil-caused mortality in a nursery laid out for routine genetic studies; the conditions were far less than ideal for a study of insect resistance. The nursery beds had been disrupted before the weevil attack occurred. Much of the stock had been lifted for transplanting to field plantations. Thus, mortality data could be obtained only for those progenies still represented in the nursery. We could compare differences in mortality

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<sup>1/</sup> Work reported here was conducted by the former Bureau of Entomology and Plant Quarantine in cooperation with the Forest Service until the Department of Agriculture was reorganized in 1953. Thereafter it was continued by the Division of Forest Insect Research of the Forest Service.

of progenies only (1) where progenies happened to be included in the same genetic test, (2) where not too many of the trees had been lifted for outplanting, (3) where enough trees had been planted to give a reliable base for estimation of mortality, and (4) where weevil attack was sufficiently intense to kill many trees. The different number of trees in each experiment complicated the problem further. The concentration of weevil attacks in tests containing highly susceptible progenies also caused complications.

#### Variable Susceptibility of Pinus ponderosa Laws.

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Miller (1950, p. 9) reported his tests in which weevils were confined to test trees in cages and his observations of trees attacked naturally. He wrote: "Ponderosa and Jeffrey pines were found to be generally susceptible, but between individual trees of each species there was wide variation in resistance to weevil attack." The progenies of one particular ponderosa pine growing on the grounds of the Institute of Forest Genetics were generally quite susceptible.

Miller's statement was based in part on his observations of mortality due to weeviling in beds of the Institute's 1946 nursery. All of these 1946 experiments, except experiments 22 and 30, were laid out in a replicated randomized plot design. A progeny row across the nursery bed represented a plot. Experiments 22 and 30 were laid out in modified latin square designs. Seven of the nursery beds were planted for a comparison of early growth behavior of eight intraspecific ponderosa pine progenies (table 1). These progenies resulted from controlled pollinations of two trees growing naturally in the vicinity of the Institute (El Dorado County, California). The pollen used in producing these progenies had been collected from planted trees growing in the arboretum at the Institute. Wind pollinated seed from one El Dorado tree was included as the El Dorado pollen source.

Observations of the weeviling in these progenies were started in 1949. The trees then were in their fourth year of growth. Miller tallied the mortality occurring during the 1949 and 1950 growing seasons (table 1 and 2). I subjected these data to statistical analyses. Chi-square values were computed from the data in a four-fold table according to the formula of Snedecor (1946, p. 199). These values have only 1 degree of freedom: values in excess of 3.84 would be encountered less than once in 20 random samples drawn from the distribution specified by the null hypothesis. Values in excess of 6.635 would be encountered less than once in 100 such samples.

Some significant effects of pollen source on progeny mortality were found (table 1). Within each experiment the local El Dorado progeny or a hybrid with an El Dorado parent suffered less mortality than did the exotic progeny being compared. Thus, progenies of parents native to the test area suffered less than progenies having exotic genes. Only comparisons of mortality within experiments can

Table 1.--Mortality of ponderosa pine progenies caused by Cylindrocopturus  
eatonii during 1949 and 1950 in the 1946 nursery

Experi- ment	Seed parent	Pollen parent	Living	Dead	Mortality	Chi <sup>2</sup>
			Percent	Value	Prob.	
21	El Dorado 4B-56	x Cle Elum, Wash.	60	37	38.1	
	"	x El Dorado	73	24	24.7	3.443 >0.05
23	"	x Cle Elum, Wash.	62	22	26.2	
	Chelan, Wash.	x Wind (IFG)	48	39	44.8	5.682 <0.05
24	El Dorado 4B-56	x Monument, Colo.	79	14	15.1	
	Monument, Colo.	x Wind (IFG)	2	20	90.9	45.585 <0.01
25	El Dorado 4B-56	x Montana	35	29	45.3	
	"	x Wind (IFG)	62	15	19.5	9.694 <0.01
26	El Dorado 4B-56	x Santa Cruz, Calif.	54	41	43.2	
	"	x Wind (IFG)	77	22	22.2	8.759 <0.01
27	El Dorado 4B-56	x Crater Lake, Ore.	47	33	41.2	
	"	x Wind (IFG)	72	23	24.2	5.038 <0.05
28	El Dorado 4B-56	x British Columbia	50	48	49.0	
	"	x Wind (IFG)	69	31	31.0	5.944 <0.05
29	El Dorado 4B-56	x Grants Pass, Ore.	63	32	33.7	
	"	x Wind (IFG)	70	26	27.1	0.696 >0.05
31	El Dorado 15-43	x Grants Pass, Ore.	95	2	2.1	
	Crater Lake, Ore.	x Wind (IFG)	59	2	3.3	0.002 >0.05
32	El Dorado 15-43	x Cle Elum, Wash.	50	14	21.9	
	Chelan, Wash.	x Wind (IFG)	52	33	38.8	4.104 >0.05

Table 2.--Mortality (during 1949 and 1950 in the 1946 nursery) of ponderosa pine progenies derived from two seed trees pollinated with pollen from five different geographic sources

Pollen sources :	Seed tree	
	El Dorado 4B-56 (experiment 22)	El Dorado 15-43 (experiment 30)
	Percent	Percent
Cle Elum, Wash.	47.4	0.0
Monument, Colo.	30.0	0.0
British Columbia	30.8	10.0
Crater Lake, Ore.	25.0	10.3
Grants Pass, Ore.	31.6	2.6

be made. Comparisons of geographic differences between experiments listed in table 1 would be invalid biologically. This is because of the inexplicable concentration of attacks in certain experiments.

However, two of the experiments, 22 and 30, were suitable for studying geographic differences in susceptibility. In neither of these were significant mortality differences associated with pollen source. Chi-square analyses were made of the data (table 2). No significant differences in mortality between pairs of progenies derived from these five different pollen sources were found.

The effect of seed parent on progeny susceptibility was shown to be highly significant from one analysis (table 2). A variance analysis showed that the progenies of one seed tree, El Dorado 4B-56 in experiment 22, exhibited the highest mortality. The progenies of the second seed tree, El Dorado 15-43 located in experiment 30, suffered only slight mortality. Whether the first were highly susceptible or, conversely, whether the second were highly resistant is impossible to determine. Furthermore, the discrepancy in mortality might just have been due to the location of the two experiments in the nursery. Yet, the highly significant difference in mortality justified the formulation of a working hypothesis.

Mortality in other experiments in this 1946 nursery (table 1) gives additional evidence to support this hypothesis. These same two seed trees are crossed with one pollen in experiments 29 and 31. Comparing these experiments, which were in fairly close proximity in the nursery beds, one finds a striking difference in mortality. Again less mortality was observed in progenies of El Dorado 15-43. These seed trees transmitted different levels of resistance to their progenies. This difference might be attributed to the difference in seed trees.

However, the difficulty in trying to work only from observations of uncontrolled attacks soon became apparent. These same two seed trees are crossed with another pollen in experiments 23 and 32. No such obvious seed parent difference is found between experiments 23 and 32, which were far apart in the nursery. This pair of experiments neither lends support to our hypothesis nor contradicts it.

These pairs of experiments and others illustrate two problems in studies of pest resistance. First, we cannot distinguish between the experiment location in the nursery and the seed trees involved in the experiments; and second, we cannot determine whether or not progenies in all experiments were attacked equally. Uncontrolled attacks by most pests tend to be clumped together. A good example of this phenomenon was the mortality in experiments 11 and 12 in the 1946 nursery (table 3). These experiments were situated side by side in the nursery bed. The progenies were nearly identical; yet, mortality was high in one experiment and low or nonexistent in the other experiment. The mortality in experiments 42 and 43 of the 1950 nursery (table 5) showed a similar pattern. This grouping of natural attacks precludes the use of a casual approach to the detection of resistance. Future controlled tests to evaluate resistance must assure uniform exposure of progenies and must preclude chance escape from attack. The caged confinement of uniform populations of insects on each progeny most nearly satisfies these requirements.

Table 3.--Natural mortality caused by Cylindrocopturus eatoni during 1949 and 1950 in Jeffrey pine and Jeffrey backcross-hybrid progenies grown in the 1946 nursery

Experi- ment :	Seed parent	: Pollen : parent	: Living : Dead	Mortal- ity		Chi <sup>2</sup> Percent	Value	Prob.
11	jeffreyi-El Dorado 1-14	x (J x C) <sup>1/</sup>	194	1	0.5	4.577	< 0.05	
		x Wind	199	9	4.3			
12	jeffreyi-El Dorado 1-14	x (J x C)	108	3	2.7	26.587	< 0.01	
		x Wind	91	36	28.3			
13	jeffreyi-El Dorado 5-3	x (J x C)	66	0	0.0	2.278	> 0.05	
		x Wind	83	5	5.7			

<sup>1/</sup> Natural hybrid P. jeffreyi x P. coulteri, Idyllwild, Riverside County, Calif.

Table 4.-Natural mortality caused by *Cylindrocopturus eatoni* in ponderosa pine and ponderosa  $F_1$  hybrid progenies (Total number of trees in each progeny shown in parentheses)

Ponderosa:		Nursery:		Ponderosa 2/		Pollen parent	
Seed 1/	tree	Engelmanni	Ponderosa 2/	3/	Chi $^2$	Arizonica	Ponderosa 2/
number	year	Mortality	Mortality	3/	Chi $^2$	Mortality	3/
		Percent	Percent			Percent	
12-1	1946	14	(29)	3	(38)	1.571	--
4B-56	1950	17	(60)	0	(94)	14.122	21 (58)
4B-62	1950	22	(119)	3	(153)	23.314	12 (51)
4B-63	1950	18	(51)	1	(42)	4.116	--
15-6	1950	34	(97)	2	(145)	44.367	4 (75) 1 (89)
15-32	1950	18	(113)	1	(135)	20.688	10 (58) 9 (130)

Scopulorum:		Ponderosa 2/		Pollen parent	
Seed 1/	tree	Arizonica	Ponderosa 2/	Chi $^2$	Chi $^2$
Mortality	Mortality	Mortality	Mortality	Mortality	Mortality
Percent	Percent	Percent	Percent	Percent	Percent
12-2	1949	--	--	--	--
4B-57	1949	--	--	--	--
4A-6	1949	10	(63)	4 (25)	0.182 (25)
4B-58	1949	33	(33)	3 (32)	7.944 (32)
36-13	1949	18	(33)	3 (30)	2.166 (30)
4B-63	1950	14	(42)	6 (62)	0.982 (62)
15-32	1950	1	(110)	0 (134)	-- (134)

1/ All seed parents from El Dorado County, California.  
2/ All ponderosa pollinations were achieved through natural wind pollination of the native seed trees.

3/ Chi  $^2$  values in excess of 3.84 have a probability of occurrence  $< 0.05$ ; those in excess of 6.635  $< 0.01$ .  
4/ *Pinus montezumae* pollen was used in making this particular hybrid.

Table 5.--Natural mortality of progenies of reciprocal crosses  
by Cylindrocopturus eatoni

Experi- ment	Seed tree	Pollen parent	Living	Dead	Mortality	Chi <sup>2</sup>	
			No.	No.	Pct.	Value	Prob.
42	Ponderosa-El Dorado 36-13	x <u>scopulorum-</u> Lyons, Colo.	27	9	25	0.544 >0.05	
	<u>Scopulorum-</u> V70 1/	x <u>ponderosa-El</u> Dorado 36-13	11	7	41		
43	<u>Scopulorum-</u> V73 1/	x <u>ponderosa-El</u> Dorado 36-13	30	0	0	-- --	
	Ponderosa-El Dorado 36-13	x <u>scopulorum-</u> Lyons, Colo.	33	0	0		

1/ Trees growing in the Institute arboretum originally obtained as 2-0 stock from a nursery at Monument, Colorado; seed source is unknown.

In the light of these difficulties, our hypothesis that the progenies of individual seed trees differ in their susceptibility must be held as tentative. It can be confirmed or refuted only by additional evidence. Such evidence should be forthcoming from studies now underway at the Institute. These studies are well designed for tests of weevil resistance. This objective is paramount right from the outset of controlled pollinations through the design of the nursery layout to the forced weevil attacks in the nursery.

Our experience shows that one cannot detect resistance through observations of natural mortality. For without controls to assure uniformity of attack, one cannot distinguish between inherent resistance and chance escape from attack. Our results apply not only here but to all attempts to select trees resistant to pests and climatic extremes. Results of observational studies can serve only as guides to the design and conduct of controlled experiment aimed at detecting resistance.

Differences in mortality of progenies of different ponderosa pines have great practical significance. When such differences first were found, hope ran high that we could find highly resistant individuals, such as El Dorado 15-43 seemed to be. Unfortunately, progenies of this particular tree have not been included in later observations; its apparent resistance remains to be confirmed. None of the other

ponderosa progenies seem to fulfill our first hopes. Rather, observations of the available progenies from year to year indicate that most ponderosa pine progenies have about the same level of inherent resistance. The progenies of El Dorado 4B-56 are exceptions. Repeated observations indicate these progenies generally are more susceptible than those of other ponderosa pines.

Instead of finding more resistant ponderosa pines, we found that at least one tree seemed to be quite susceptible. If experiments now underway confirm this conclusion, then this tree and others like it probably should be avoided as seed trees. Their progenies would possess an intolerable degree of weevil susceptibility. However, the recognition of seed trees transmitting high susceptibility does not have a high value to a tree improvement program. The need is for seed trees which transmit high resistance.

#### Resistance of Interspecific Hybrids

In the beginning Miller forced weevils to attack caged trees. He found: (1) that the species of pines varied in their resistance to the pine reproduction weevil and (2) that an interspecific hybrid usually was intermediate in resistance to its parent species. Pinus coulteri D. Don was immune to even the heaviest attacks. Pinus ponderosa Laws and P. jeffreyi Grev. and Balf. showed a variable degree of resistance. The list of highly susceptible species included P. ponderosa varieties scopulorum Engelm. and arizonica (Engelm.) Shaw, P. engelmannii Carr., P. montezumae Lamb., and P. contorta var. latifolia Engelm. Miller also confirmed this species susceptibility from observations of natural weevil infestations.

In 1949 and again in 1950 Miller made observations of natural infestations in genetic tests of hybrids. In each experiment the interspecific hybrid was pitted against the wind-pollinated progeny from the same tree. The progenies of two different individuals of P. jeffreyi backcrossed to a natural hybrid, P. jeffreyi x P. coulteri were represented in one case (table 3). Chi-square analyses of 3 experiments showed the backcross hybrid to possess a significantly higher degree of resistance than open-pollinated Jeffrey progenies.

The difference in frequency of mortality between two identical tests is demonstrated in experiments 11 and 12. This difference shows again why comparisons of mortality between experiments cannot be made. If such comparisons are made, only tentative conclusions can be drawn, as genetic differences in susceptibility are confounded with experiment location.

Miller (1950) reported that several other hybrids exhibited considerable susceptibility. Among these were  $F_1$  hybrids, P. ponderosa x P. ponderosa var. scopulorum, P. ponderosa x P. engelmannii (apachea), and P. ponderosa x P. ponderosa var. arizonica. Our observations of natural mortality in the 1946, 1949, and 1950 nurseries support Miller's conclusion (table 4). Most of these  $F_1$  hybrid

progenies exhibited a significantly higher degree of susceptibility than did the wind pollinated ponderosa progenies with which they were compared. The hybrid P. ponderosa x P. montezumae was observed for the first time in the 1950 nursery. This vigorous hybrid too showed significantly increased susceptibility over the ponderosa checks.

Two tests of geographic reciprocal crosses between P. ponderosa and its variety scopulorum were included in the 1949 nursery (table 5). Mortality did not differ significantly between the reciprocal progenies within either of these experiments; no maternal effect was apparent. Here again, though, we have a striking discrepancy in mortality between practically identical adjacent experiments. This further illustrates the variation in the uncontrolled attack pattern of this weevil.

#### Escape Versus Resistance

Miller and I saw time and again how entire experiments escaped attack. We have asked ourselves: Within an experiment or even within a progeny, is apparent resistance merely the result of escape from attack? Chance escape of an entire progeny within an experiment would not seem likely; in each experiment progenies were located according to designs incorporating replication and randomization. Nevertheless the question still remained. Was attack equal?

Attack by this weevil is a double-barreled process. First the weevils puncture and feed on the needles. Later, on the same or another tree, they make punctures on the stem and oviposit in the cortex.

I studied frequency of attack in conjunction with assessment of the 1952 mortality in the 1949 and 1950 nursery beds. The procedure for study was simple. Working down the length of a nursery bed, I counted the number of living and killed individuals in each row across the bed. All individuals in a row were of the same parentage. The pattern of insect attack was examined more closely on one live and one dead individual in each row. First, the number of needle punctures on 3 fascicles of needles taken from the growth of the current year were counted. Second, the stem of the tree was bent between the legs of the observer; only half of the main stem then was visible. At some of the stem punctures a resin drop had appeared on the bark. The number of these drops on each year of growth was recorded. Finally, the height growth of the main stem in each year was measured and recorded. These data were compiled to give two measures of frequency of attack on each tree: (1) the number of needle punctures per 9 needles (usually 3 fascicles of 3 needles) and (2) the number of resin drops per linear inch of the 1- and 2-year-old portions of the stem.

The frequency of attack on different progenies was analyzed. The 2-year-old part of the stems of living trees was most heavily attacked; hence the data on frequency of resin drops on these stem-segments was used. Separate analyses of variance were made for 13

experiments in the 1949 and 1950 nurseries. No basis was found for rejecting the null hypothesis that within each experiment the progenies were equally attacked. Observed differences in mortality probably reflect real differences in inherent progeny resistance.

None of the progenies suffered significantly more than others with which it was being compared. However, some of the variance ratios which were obtained verged on being significant at the 0.05 probability level. If one were to sample these progenies both more intensively and more extensively, a significant preference by the weevil for certain progenies might be demonstrated.

The frequency of attack on individual surviving and killed trees was analyzed next. For this purpose, data were selected to permit comparisons within progenies. Pairs of living and killed trees from the same nursery rows were used. For 143 pairs, I found a highly significant difference in the number of needle punctures. The killed trees had about twice as many needle punctures (7.31) as their living counterparts (4.89).

The frequency of needle-feeding causing these punctures may have an influence on susceptibility. Miller was able to demonstrate that the weevils must feed on the foliage to attain sexual maturity. He found that newly emerged weevils would attack the stem to oviposit only after feeding on needles. This obligate feeding may be coupled with the significantly higher frequency of needle attack on the killed trees and may suggest an influence of needle-feeding on mortality. Thus, observations on uncontrolled attacks indicate a promising avenue of basic research.

The frequency of stem attack also differed significantly between living and killed trees of the same parentage. Both living and killed trees on the average had many more resin drops on the 2-year-old portion of the stem than on the 1-year-old portion; therefore, I studied the frequency on the 2-year-old stems. The living trees had significantly more resin drops than the killed trees: 1.57 versus 1.07 drops per inch of stem. Again, we do not know the cause of this difference. If the frequency of resin drops were proportional to the frequency of stem attacks, one might logically expect the most heavily attacked individuals to be the ones to succumb. The reverse was true. Four possible explanations of this relationship are: (1) trees which succumb may die before the termination of the attack period; or (2) trees which succumb may not be attractive to the weevil over as long a period as the survivors; or (3) the survivors may have been able to tolerate a heavier concentration of stem attack perhaps by virtue of the lesser foliage feeding to which they were subjected; or (4) the number of resin drops per linear inch of stem may not accurately reflect the actual frequency of stem attacks on both living and dead trees. Nevertheless, without explanation of the cause, another research lead is presented.

Three principal findings appear from this study of frequency of attack. First, all progenies in an experiment were attacked rather uniformly; none seemed to have escaped attack. Second, needle-feeding was nearly twice as heavy on the trees which succumbed as it was on their surviving counterparts. This needle-feeding may play a significant part either in the selection of susceptible individuals by weevils or in conditioning susceptibility through its effect on the host. Third, frequency of stem attacks showing resin drops paradoxically was higher on surviving individuals than on those which succumbed. Additional study is needed to determine the statistical validity and the biological significance of these differences in pattern of attack on individual trees.

### Summary

A natural infestation of Cylindrocopturus eatoni in the nurseries of the Institute of Forest Genetics was followed from 1949 through 1953. The observed mortality confirmed the relative susceptibility of species and hybrids to weevils as determined from earlier forced-attack tests. Evidence was presented to support the tentative hypothesis that individual trees vary considerably in the susceptibility which they transmit to their progenies.

Progenies of intraspecific ponderosa pine crosses showed genetic variations in weevil susceptibility. Susceptibility was associated both with the geographic source of the pollen and with the individual tree used as seed parent. Progenies of exotic parents were more susceptible. On the basis of repeated observations, one tree seemed to transmit rather a high degree of susceptibility to its progenies.

Observations of natural mortality in species and hybrid progenies are reported. They confirmed the susceptibilities to weevil attack determined earlier through forced attacks. The backcross of a natural Jeffrey x Coulter hybrid to Jeffrey pine was less susceptible than straight Jeffrey pine. Wind-pollinated ponderosa pine progenies were not as susceptible as  $F_1$  hybrids between ponderosa pine and more susceptible species: P. ponderosa varieties scopulorum and arizonica, P. engelmannii, and P. montezumae.

A study of the pattern of weevil attack on needles and stems of living and killed trees disclosed three important relationships. First, within an experiment no significant differences were found between progenies in the frequency of stem attacks; chance escape from attack did not seem to have occurred. Second, needle-feeding was heaviest on trees which later succumbed to attack. Third, stem attacks seemed to be most frequent on survivors.

Perhaps most important, this study illustrates some features of observations in a natural pest infestation. First, one can confirm other more critical experimental results. Second, one can uncover new leads for more refined research. Third, one can observe susceptibility although one cannot detect resistance. This leads to the fourth point:

one is severely handicapped without control of the pest and can only make tentative conclusions in many instances.

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